

# Effects of Rangeland Management on the Site Occupancy Dynamics of Prairie-Chickens in a Protected Prairie Preserve

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**ABSTRACT** We investigated the site occupancy dynamics of greater prairie-chickens at Konza Prairie Biological Station, a protected site in northeastern Kansas that is managed for ecological research. We surveyed the site during mid-Mar to mid-May, 1981–2008, and recorded detections of birds in a grid of 6.3 ha survey plots ( $n = 187$  plots). We used multiseason occupancy models to estimate the probabilities of occupancy ( $\psi$ ) and detection ( $p$ ), and tested whether land cover in woody vegetation, and land use with prescribed fire or grazing management influenced the dynamic processes of site colonization and local extinction. Probability of detection per site was consistently  $<1$  and varied among years ( $p = 0.12$ – $0.82$ ). Site occupancy of prairie-chickens declined 40% over the study period from a high of  $\psi = 0.19 \pm 0.02$  SE in 1981 to a low of  $0.11 \pm 0.03$  in 2008, despite protection from disturbance at leks and losses to harvest. We found that different sets of environmental factors impacted the probabilities of colonization and local extinction. Probability of colonization for an unoccupied site was negatively associated with the proportion of site occupied by woodland cover ( $\beta = -1.25$ ), and was lower for grazed sites ( $\beta = -0.62$ ). In contrast, probability of local extinction was affected by a weak interaction between grazing and average frequency of prescribed fire ( $\beta = -1.01$ ), but model-averaged slope coefficients were not statistically different than 0. To conserve prairie-chickens, we recommend prairies be managed with combinations of prescribed fire and grazing that maintain a heterogeneous mosaic of prairie habitats, while preventing woody encroachment. To assess biotic responses to land management practices, field sampling should be based on occupancy models or similar techniques that account for imperfect detection. © 2011 The Wildlife Society.

**KEY WORDS** colonization, detection probabilities, greater prairie-chicken, Kansas, Konza Prairie Biological Station, local extinction, occupancy modeling, *Tympanuchus cupido*.

The Flint Hills ecoregion has been considered a stronghold for prairie-chickens and other sensitive species of grassland birds due to large expanses of relatively intact grasslands (Svedarsky et al. 1999, Pashley et al. 2000, Johnsgard 2002). However, the Flint Hills have experienced losses of tallgrass prairie through conversion to tall fescue (*Festuca arundinaceae*) and grazing-tolerant exotic grasses, by invasion of sericea lespedeza (*Lespedeza cuneata*) and other exotic species, and by exurban development (Vickery et al. 2000; Briggs et al. 2002a, 2005; Johnson and Sandercock 2010). Changes in rangeland management may also be impacting the quality and ecological integrity of tallgrass prairie. Fire suppression in some areas has led to expansion of deciduous trees from riparian gallery forests into upland areas and encroachment by eastern red cedar (*Juniperus virginiana*),

roughleaf dogwood (*Cornus drummondii*), and other woody shrubs (Knight et al. 1994; Briggs et al. 2002b, 2005). Most of the native grasslands in the Flint Hills are private lands managed for livestock production. Intensification of rangeland management with a higher frequency of prescribed burns and more intensive grazing regimes have led to ecological changes in the structural and heterogeneity of prairie plant communities, with impacts for associated wildlife species (Fuhlendorf and Engle 2001, Robbins et al. 2002, With et al. 2008).

The greater prairie-chicken (*Tympanuchus cupido*, hereafter prairie-chicken) is an obligate grassland bird and an indicator species for tallgrass prairie (Schroeder and Robb 1993, Poiani et al. 2001). Contracting distributions and declining numbers of prairie-chickens have paralleled extensive loss and fragmentation of native prairie habitats (Knopf 1994, Svedarsky et al. 1999, Westemeier and Gough 1999). Prairie-chickens are traditionally surveyed by counting birds at display arenas (leks) in spring. Lek surveys by the Kansas Department of Wildlife and Parks indicate that the Flint Hills population of greater prairie-chickens has been

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declining by 2–3% per year during the past 20–30 years (Applegate and Horak 1999, Rodgers 2010). Lek surveys may not be the best index of population size if detection of leks is imperfect, if a variable subset of the population does not attend leks, or if flush counts of birds from leks are biased low (Applegate 2000, Walsh et al. 2004, Clifton and Krementz 2006, McNew et al. 2011a). Nevertheless, estimation of fecundity and survival through intensive monitoring of radio-marked birds is costly and requires an intensive field effort. Effective wildlife management requires efficient survey techniques that produce unbiased estimates of population status, and allow investigation of the relationships between species occurrence and environmental conditions.

Occupancy models for analysis of detection-nondetection data have proven to be a useful set of tools for evaluating population status, distributional changes, and ecological correlates of the occurrence of wildlife species. MacKenzie et al. (2003) described a model for estimating the probability that a site is occupied by a species ( $\psi$ ) when the probability of detecting the species is imperfect ( $p < 1$ ). Similar to robust design models for analyses of live encounter data (Pollock 1982), the multiseason occupancy model estimates the probabilities of occupancy and detection for closed periods by repeated surveys within a season, and for open periods among consecutive seasons or years. Multiseason occupancy models allow investigation of site occupancy dynamics over time, and can be used to explore how environmental factors affect occupancy rates via the ecological processes of colonization ( $\gamma$ ) and local extinction ( $\epsilon$ ; MacKenzie et al. 2003, 2006).

We used multiseason occupancy models to examine long-term patterns of site occupancy for prairie-chickens at a tallgrass prairie preserve in northeast Kansas. We expected that population declines at our protected site would not be as great as private lands in the Flint Hills because our study area was closed to hunting, had limited disturbance from controlled public access, and was sustainably managed for ecological research. Surveys of prairie-chickens over a 28-year period in a heterogeneous landscape with a range of grassland habitats provided a unique opportunity to assess the utility of occupancy modeling in investigating site occupancy dynamics for a sensitive species of grassland bird. Our 2 main objectives were to estimate long-term patterns of occupancy and detection for prairie-chickens, and to examine the effects of rangeland management on the colonization of unoccupied sites and local extinction of occupied sites.

## STUDY AREA

Konza Prairie Biological Station (hereafter, Konza Prairie) is a 3,487 ha native tallgrass prairie preserve located in the Flint Hills ecoregion of northeast Kansas (39°05'N, 96°35'W). Since 1981, Konza Prairie has been part of a national network of Long-term Ecological Research (LTER) sites supported by the National Science Foundation. The field site is managed with a replicated experimental design in which approximately 60 experimental units (watersheds) are treated with different combinations of prescribed burning and grazing (Knapp et al. 1998). About 42% of the site is grazed by bison (*Bos bison*; 27%) or domestic cattle (*Bos primigenius*;

15%), and the rest of the site is ungrazed (58%). Grazing by bison and cattle is year- and season-long, respectively, at light-to-moderate stocking rates that have varied during 1981–2008 (E. G. Towne, Kansas State University, personal communication). Prescribed fires are usually conducted in March and April and fire-return intervals of watershed treatments range from 1 to >20 years with some variation among replicates within the same treatment. The climate is characterized by warm, wet summers and dry, cold winters, but mean annual precipitation (approx. 84 cm) is adequate to support either grassland or woodland vegetation (Knapp et al. 1998). Disturbance from grazing, fire, and climatic variability creates 4 structurally different habitat types: burned prairie, unburned prairie, attenuated forest, and gallery forest (Zimmerman 1993). Most of Konza Prairie is comprised of native tallgrass prairie (>85%), but spread of woody shrubs and trees in experimental units with long fire-return intervals has increased total woodland cover from 10% in 1983 to 13% in 2009 (Konza LTER, unpublished data).

## METHODS

### Prairie-Chicken Surveys

At the outset of the LTER program in 1981, Konza Prairie was mapped with a grid of 250 × 250-m cells (6.3 ha,  $n = 560$ ) that were used for different types of long-term ecological sampling, including counts of prairie-chicken numbers. Prairie-chicken surveys were conducted over a 28-year period during March–May of 1981–2008. No surveys were conducted in 1990. Birds were counted 2–4 times during March–May by driving the 22-km circular access road and a network of roads among boundaries between experimental units. Direction of travel was alternated between clockwise and counterclockwise on consecutive surveys to control for diurnal changes in lek activity after sunrise. Grid cells were defined as survey sites as per MacKenzie et al. (2006). Only grid cells adjacent to access roads were surveyed ( $n = 186$  sites). Surveys began at sunrise, lasted approximately 2 hr and were conducted under conditions without rain and low winds (<25 km/hr) to maximize detection of birds from calls and behavioral displays. Maintaining speeds <20 km/hr, observers counted all birds and recorded the grid cell for all detections of prairie-chickens. If birds were flushed by observers, care was taken to avoid double-counting of birds that had moved to a different grid cell. Counts included birds displaying at lek sites and birds foraging at non-lek sites, but bird activity was not recorded separately in the field notes.

### Habitat Covariates

We considered 4 environmental correlates for the effects of rangeland management and land cover change on the probabilities of colonization and local extinction for prairie-chickens during the 28-year study period: fire return interval, average fire frequency, grazing regime, and land cover. Fire-return intervals were set at 1, 2, 4, 10, or 20 years for the experimental burn treatments, but realized fire return intervals for a given experimental unit were sometimes different. Entry of units into the experiment was staggered at the start

of the LTER program, some units were burned off-schedule if lightning strikes caused wildfires, and some units were not treated with fire or changed treatment during the course of the experiment. Thus, we used long-term records from the Konza Prairie LTER (2010) to reconstruct the management history for each experimental unit and survey site. We calculated the fire-return interval as the number of years since a site was burned at the time of the spring surveys (0–28 yr), and the average fire frequency as the average number of fires per year ( $0.5 = \text{burned 14 times in a 28-yr period}$ ). Fire-return intervals evaluated short-term management actions, whereas average fire frequency described the long-term management for an experimental site. We also used the long-term records to determine the grazing regime for each experimental unit. Bison and cattle grazing had similar effects on site occupancy of prairie-chickens in preliminary analyses (not shown), and we opted to use a single dummy variable to indicate whether a site was grazed or ungrazed.

We obtained land cover data for Konza Prairie for 5-year intervals from 1983 to 2009 from cloud-free Landsat 5 TM imagery (Path 28/Row 33;  $30 \times 30$  m pixels, 0.09 ha; U.S. Geological Survey 2010). We acquired 3 satellite images within the same growing season (Mar–Aug) for each year. However, due to a lack of cloud-free imagery in 1983 and 1984, we used 1 of the 3 Landsat images from the non-growing season (Jan) in these years. We clipped Landsat images to the extent of the Konza Prairie boundary and visually inspected to confirm that the images were spatially registered to each other. Next, we combined 4 Landsat bands, 3 (blue), 4 (green), 5 (visible red), and 7 (near infrared), from each of the 3 time periods per year into a single 12-band image using ENVI 4.5 (ITT Visual Information Solutions, Boulder, CO). Price et al. (1997) showed these 4 spectral bands were effective for identifying habitats in Kansas with multi-temporal landcover classification schemes. To maintain consistency in classification, we created training sites that were suitable for all of the years of Landsat imagery and validated using aerial photographs of the area. We used a supervised maximum-likelihood classifier to assign each pixel in the 12-band Landsat composites to 1 of 4 land cover classes: grassland, woodland, cultivated agriculture, and water. We were unable to discriminate between shrubland and forest in the woodland cover class. To assess the accuracy of grassland and woodland classes, we compared the assigned land cover classes of 70 random points within the study boundary to aerial photographs. Our land cover classification technique correctly classified woodland and grassland pixels 70% and 98% of the time, respectively (kappa values ranged from 0.73 to 0.85). Of pixels that we misclassified, 76% occurred in areas that contained both grass and woodland cover in the same pixel.

We uploaded land cover data to ArcInfo 9.3 (Environmental Systems Research Institute, Redlands, CA). We overlaid a vector with a grid of  $250 \times 250$ -m cells (6.3 ha,  $n = 560$ ) corresponding to prairie-chicken survey sites onto each land cover dataset. Prairie-chickens did not occupy sites classified as cultivation or water, and used upland sites with either grassland or woodland cover. The propor-

tion of a survey site in grassland and woodland cover were inversely related, so we included woodland cover only as a covariate in our occupancy analyses. We used the zonal statistics tool to summarize the number of pixels of woodland for each survey site (approx. 69 pixels per 6.3 ha grid cell). We estimated the proportion of woodland for each survey site directly from our land cover data at 5-year intervals in which land cover data were created (1983, 1988, 1993, 1998, 2003, and 2009). We used linear interpolation to estimate woodland cover for intervening years for every survey site during 1983–2008.

### Data Analysis

Counts of prairie-chickens at 6.3-ha survey sites were transformed into encounter histories where surveys were coded as birds detected (1) or not (0). For each set of survey sites, prairie-chickens were observed with the probability  $\psi p$ , where  $\psi$  is the proportion of sites occupied and  $p$  is the probability of detection, conditional upon occupancy. Nondetection could occur if prairie-chickens were absent ( $1 - \psi$ ), or if birds were present but not detected ( $\psi \times [1 - p]$ ). Failure to detect birds could be caused by flushing of birds from lek sites by predators or by changes in the site use of foraging birds. Prairie chickens are difficult to detect if they are not attending leks or flying. A foraging bird may be detected if it is close to the survey route but not if it is far away. We found in a previous study that lek attendance was not negatively impacted by our presence at leks (McNew et al. 2011a).

Multiseason occupancy models required 4 assumptions which were met in this study: 1) the population of interest is closed to additions or losses within each season; 2) detection of prairie-chickens at each site is independent; 3) a site is never classified as occupied when it is not; and 4) there is no unmodeled heterogeneity in occupancy or underlying dynamic processes. The first assumption was satisfied because prairie-chicken movements are limited in spring and intervals among consecutive surveys within the same season were short (Robel et al. 1970, Nooker and Sandercock 2008). Assumptions 2 and 3 were met for prairie-chicken surveys because we took steps to avoid double-counting and no other species in our study area has the same behavior or vocalizations. We tested the fourth assumption by modeling dynamic probabilities as a function of different environmental covariates. Other potential sources of bias are that detection and occupancy may be associated with distance of sites from the survey route (i.e., occupancy may be higher at sites away from roads) or the number of observers. We reject the first bias because survey roads were unimproved and access was limited to just Konza researchers. In addition, lek occurrence was unrelated to distance to unimproved roads (Gregory et al. 2011) and locations of radio-marked females were not related to distance to unimproved roads in the northern Flint Hills (L. B. McNew, Kansas State University, unpublished data). Most surveys were conducted by a single observer: the driver. We accept that drivers may have lower detection rates than non-drivers. However, this bias does not negatively affect our occupancy estimates be-

cause we estimated detection probabilities for each survey and study unit and adjusted accordingly. We expected detection to increase with the number of observers but not occupancy. We conducted our occupancy modeling in 2 steps. First, we estimated annual probabilities of site occupancy and detection for prairie-chickens at Konza Prairie. Second, we used a constrained model to examine fire, grazing, and woodland cover as environmental covariates influencing the probabilities of site colonization and local extinction.

*Site occupancy and detection.*—We used Program PRESENCE (ver. 3.0; Patuxent Wildlife Research Center, United States Geological Survey, Laurel, MD) to build and evaluate occupancy models using Akaike's Information Criterion adjusted for small sample sizes ( $AIC_c$ ) in an information-theoretic framework (Burnham and Anderson 2002). We used an alternative parameterization of the unconditional multiseason approach developed by MacKenzie et al. (2003) to model seasonal occupancy ( $\psi$ ) and local extinction ( $\varepsilon$ ), corrected for the probability of detection ( $p$ ). Colonization probability ( $\gamma$ ) was derived using (MacKenzie et al. 2006:199)

$$\gamma_t = \frac{\psi_{t+1} - \psi_t(1 - \varepsilon_t)}{(1 - \psi_t)}$$

Our main objective was to determine how occupancy and local extinction probabilities changed over time. Therefore, we limited our analysis to include only sites where a prairie-chicken was detected at least once during any survey in the entire 28-year study ( $n = 112$  sites). Conditioning on detection may inflate estimates of site occupancy at Konza Prairie, but should provide better estimates of long-term trends in site occupancy by discarding sites not used by prairie-chickens. We developed a suite of a priori models representing annual and survey-specific effects as well as linear and non-linear time trends. For example,  $\psi_{\text{linear}}, \varepsilon_{\text{year}}, p_{\text{season, survey}}$  represents a model where occupancy ( $\psi$ ) was constrained to be a linear trend (increasing or decreasing) over the 28-year study, local extinction ( $\varepsilon$ ) varied among years (but not as a trend), and detection probability ( $p$ ) varied among sampling occasions. Large groups of prairie-chickens may show fidelity to lek or foraging sites and be easier to detect, and we included the survey-specific count data as a covariate to test the effects of abundance on the probabilities of occupancy and detection.

A usual first step in mark-recapture modeling is to use goodness-of-fit (GOF) tests to estimate a variance inflation factor ( $\hat{c}$ ) to control for a lack of fit between the starting global model and the encounter histories. We were unable to correct for potential lack of fit because no formal GOF test exists for multiseason occupancy models (MacKenzie et al. 2003). We assumed that overdispersion was negligible and proceeded with model selection based on Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ). We considered models with  $\Delta AIC_c$  values  $\leq 2$  to be equally parsimonious and used Akaike weights to assess relative support for different models ( $w_i$ ). Occupancy, local

extinction, and detection probabilities were estimated from the minimum- $AIC_c$  model using maximum likelihood integration or model averaging when more than 1 model was supported (Burnham and Anderson 2002, MacKenzie et al. 2006). In addition, we derived the finite rate of change in site occupancy ( $\lambda_t$ ) per year as

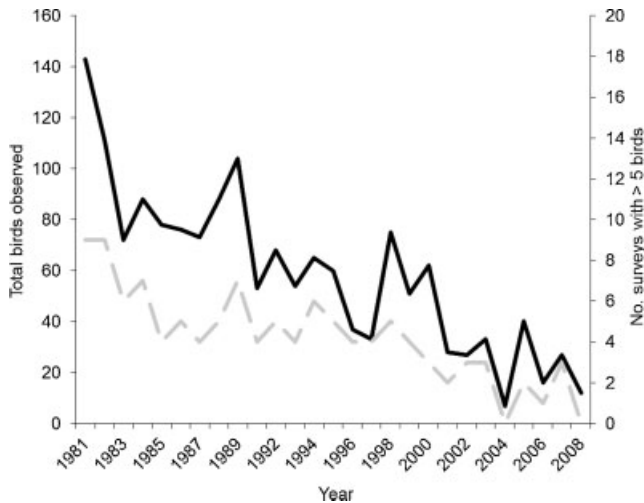
$$\lambda_t = \frac{\psi_{t+1}}{\psi_t}$$

and used the delta method to calculate standard errors and confidence intervals (MacKenzie et al. 2006:74). Estimates of  $\lambda_t < 1$  indicate declines in site occupancy, whereas  $\lambda_t \geq 1$  indicate a stable or increasing population.

*Environmental correlates of colonization and local extinction.*—To evaluate effects of environmental factors on the dynamic processes of site occupancy, we developed a second suite of multiseason occupancy models. We used the original model parameterization described by MacKenzie et al. (2003) where  $\psi$  was held constant at an initial occupancy level, and the dynamic processes of occupancy, colonization ( $\gamma$ ), and local extinction ( $\varepsilon$ ) were then modeled separately. We held occupancy constant at values in the first year of the study (1983), and fit a suite of 25 candidate models in which  $\gamma$  and  $\varepsilon$  were modeled as a function of 4 different site-specific environmental factors: fire-return interval, average fire frequency, grazing treatment, and proportion of woodland cover. We considered main effect models (+) and factorial models with interactions ( $\times$ ) as well as constant (null) models. Woodland proportion was arcsin-square-root transformed and then  $z$ -transformed. We also evaluated quadratic functions to assess non-linear responses of  $\gamma$  and  $\varepsilon$  to variation in the environmental covariates. Landcover data derived from Landsat 5 imagery were available for 1983–2008, and we discarded prairie-chicken survey data from the first 2 years of the study for analyses of covariates (1981–1982). Estimates of site occupancy, detection, colonization, and local extinction were either taken from the minimum- $AIC_c$  model or calculated by model-averaging where appropriate (Burnham and Anderson 2002, Moore and Swihart 2005).

## RESULTS

During March–May of 1981–2008, 2–4 surveys were conducted per year at each of the 6.3 ha survey sites where prairie-chickens were detected at least once in the 28-year study period ( $n = 112$  sites). The peak annual count was 142 birds in 9 groups of  $\geq 5$  birds in 1981, and the lowest count was 18 birds with no groups  $\geq 5$  birds in 2008. The mean number of prairie-chickens per site decreased by 3.8% per year from  $1.5 \pm 0.4$  (SE) birds per site in 1981 to  $0.09 \pm 0.03$  birds per site in 2008 (Fig. 1). Conversely, the mean proportion of woodland cover at survey sites increased from  $0.05 \pm 0.01$  in 1983 to  $0.08 \pm 0.01$  in 2008. Woodland cover increased at 42% of sites, decreased at 20% of sites, and did not change at 38% of the sites over the 28-year study period. During the study period, 42% of sites were grazed by bison or cattle, and 58% were ungrazed.



**Figure 1.** Maximum number of greater prairie-chickens observed (solid line) and the number of surveys in which  $\geq 5$  birds were observed together (dashed line) per survey year at Konza Prairie Biological Station, Kansas, 1981–2008.

### Occupancy and Detection

We found strong evidence that the probability of detection varied among years ( $p_{\text{year}}$ ;  $w_i > 0.99$ ; Table 1). Estimates of detection ranged from  $p = 0.12 \pm 0.05$  SE to  $0.82 \pm 0.07$ , but did not vary in an annual linear trend. Two models were considered equally parsimonious ( $\Delta\text{AIC}_c \leq 2$ ) and the probability of site occupancy varied in linear trend in both models (Table 1). Model averaged estimates indicated that the probability of site occupancy declined over the 28-year study period ( $\beta = -2.31$ , 95% CI =  $-4.93, 0.30$ ; Table 2). Overall, site occupancy decreased by 40% from  $\psi = 0.19 \pm 0.02$  (SE) in 1981 to  $0.11 \pm 0.03$  in 2008 (Fig. 2).

A model with a linear effect of local extinction was parsimonious and had 29% of the relative support of the data (Table 1). The annual probability of local extinction increased from  $\varepsilon = 0.52$  per site in 1981 to 0.68 in 2008 (Fig. 3) but the slope coefficient did not significantly differ from 0 ( $\beta = 2.7$ , 95% CI =  $-1.61, 7.01$ ). Conversely, derived estimates of site colonization showed a weak decreasing linear trend from  $\gamma = 0.11 \pm 0.03$  in 1981 to  $0.09 \pm 0.03$  in 2008. The average rate of change in occupancy derived from the top model was  $\lambda = 0.97$  (95% CI =  $0.96, 0.99$ ), indicating significantly decreasing occupancy at  $-3\%$  per

**Table 2.** Model-averaged slope parameter estimates ( $\hat{\beta}$ ), standard errors, and 95% confidence intervals for probabilities of occupancy, colonization, and local extinction for greater prairie-chickens at Konza Prairie Biological Station, 1981–2008.

Variable	$\hat{\beta}$	SE	95% CI
Occupancy			
Intercept	−1.45	0.18	−1.81, −1.10
Linear	−2.31	1.24	−4.93, 0.30
Colonization			
Intercept	−3.30	0.16	−3.61, −3.00
%Woodland	−1.25	0.44	−2.12, −0.37
Grazing	−0.62	0.23	−1.08, −0.16
Local extinction			
Intercept	−0.76	0.29	−1.33, −0.18
Fire frequency	0.24	0.43	−0.60, +1.07
Grazing	0.87	0.77	−0.63, 2.38
Interaction	−1.01	1.44	−3.83, +1.81

year over the 28-year period. We found no evidence that the probabilities of occupancy or detection were influenced by counts of the prairie-chickens detected by observers ( $\psi_{\text{count}}$ ,  $p_{\text{count}}$ ;  $w_i < 0.01$ , Table 1).

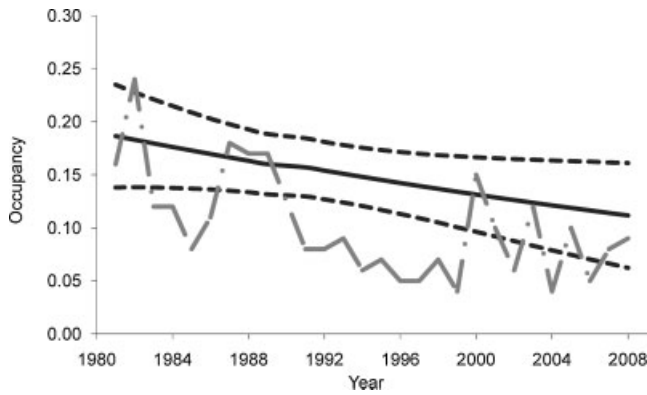
### Environmental Correlates of Colonization and Local Extinction

Before modeling the effects of the environmental covariates, we explored covariation among the different factors. We expected that woodland cover might be positively related to fire-return interval. However, fire-return intervals explained only half of the variation in the proportion of woodland cover among sites ( $r^2 = 0.50$ ,  $\text{df} = 1$ ,  $n = 150$ ,  $P < 0.001$ ). The 30-m spatial resolution of our landcover data prevented us from correctly classifying patches of woody vegetation that were smaller than half a pixel ( $< 0.05$  ha), but small shrub patches were more common with longer fire-return intervals (Briggs et al. 2002a). Thus, we retained all 4 environmental covariates in our models.

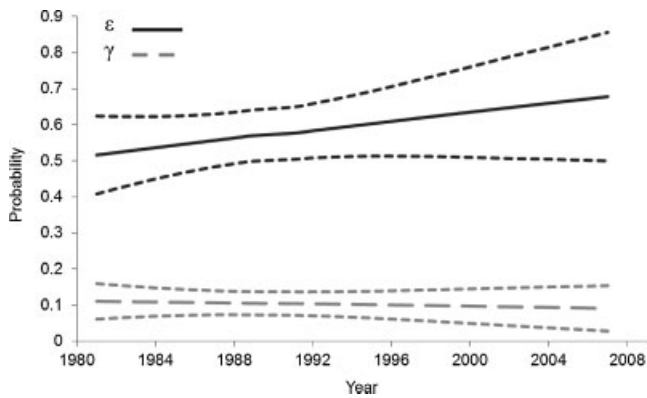
In our second set of models, 3 models were equally parsimonious ( $\Delta\text{AIC}_c \leq 2$ ) and had  $w_i = 0.59$  of the relative support of the data (Table 3). We modeled probability of detection as year-specific ( $p_{\text{season}}$ ;  $w_i > 0.99$ ). All models indicated that probability of an unoccupied site being colonized ( $\gamma$ ) was influenced by the proportion of the site in woodland cover and the grazing treatment (Table 3). Model-averaging indicated that site colonization was negatively

**Table 1.** Model selection results for probabilities of occupancy ( $\psi$ ), local extinction ( $\varepsilon$ ), and detection ( $p$ ) for greater prairie-chickens at Konza Prairie Biological Station, Kansas, 1981–2008. Models ranked by the difference ( $\Delta\text{AIC}_c$ ) between the model with the lowest Akaike's Information Criterion for small samples ( $\text{AIC}_c$ ) and the  $\text{AIC}_c$  for the current model ( $K$  = number of model parameters,  $w_i$  = Akaike weight).

$\psi$	$\varepsilon$	$p$	$K$	$\text{AIC}_c$	$\Delta\text{AIC}_c$	$w_i$
Linear	Constant	Year	30	3000.2	0.00	0.567
Linear	Linear	Year	31	3001.5	1.34	0.290
Quadratic	Constant	Year	30	3004.3	4.14	0.071
Constant	Constant	Year	29	3004.4	4.16	0.000
Constant	Constant	Constant	3	3016.4	16.2	0.000
Linear	Constant	Year, survey	83	3170.5	170	0.000
Year	Year	Year	80	3171.3	171	0.000
Count	Constant	Year	31	4188.3	1,188	0.000
Linear	Constant	Count	5	4450.3	1,450	0.000

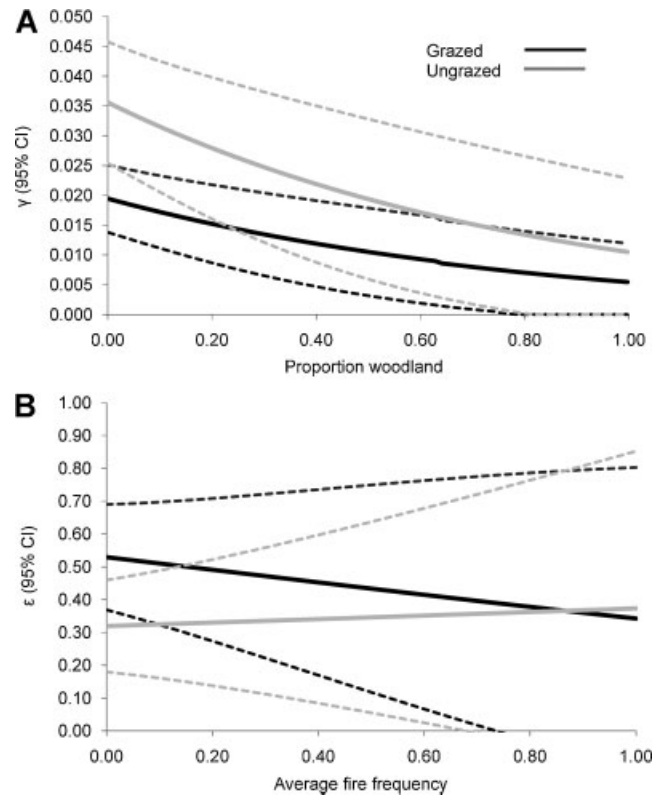


**Figure 2.** Year-specific proportion of sites with greater prairie-chickens present (naïve occupancy; dashed gray line) and probability of occupancy ( $\pm 95\%$  CI; solid black line) estimated from the parsimonious model ( $\psi_{\text{linear}}$ ,  $\epsilon_{\text{linear}}$ ,  $p_{\text{season}}$ ) for prairie-chickens at Konza Prairie Biological Station, Kansas, 1981–2008.



**Figure 3.** Estimated probabilities of local extinction ( $\epsilon \pm 95\%$  CI) and derived colonization ( $\gamma \pm 95\%$  CI) of greater prairie-chickens at Konza Prairie Biological Station, Kansas, 1981–2008. Maximum likelihood estimates calculated using the parsimonious model,  $\psi_{\text{linear}}$ ,  $\epsilon_{\text{linear}}$ ,  $p_{\text{season}}$ .

associated with the proportion of woodland cover ( $\beta = -1.25$ ,  $95\%$  CI =  $-2.12$ ,  $-0.37$ ) and grazing ( $\beta = -0.62$ ,  $95\%$  CI =  $-1.08$ ,  $-0.16$ ). Ungrazed sites were 1.8 times ( $95\%$  CI =  $1.2$ ,  $2.8$ ) as likely to be colonized as grazed sites (Fig. 4A). There was uncertainty for the



**Figure 4.** Relationships between (A) the probability of colonization ( $\gamma$ ) and the proportion of a 6.3 ha site classified as woodland, and (B) the probability of local extinction ( $\epsilon$ ) and average frequency of fire for grazed and ungrazed sites at Konza Prairie Biological Station, Kansas, 1983–2008. Average fire frequency ranged from never burned (0) to burned every year during the 28-year study period (1).

effects of environmental covariates on the probability of local extinction ( $\epsilon$ ; Table 3). The top model included a significant interaction between grazing and the average frequency of fire (Table 3) suggesting that the effects of fire frequency on local extinction may have been conditional upon whether a site was grazed or not. Models that included the effects of grazing on local extinction had  $w_i > 0.8$  of the relative support and suggested that grazed sites were more likely to be abandoned, but confidence intervals of average slope

**Table 3.** Model selection results for colonization ( $\gamma$ ) and local extinction ( $\epsilon$ ) of greater prairie-chickens at Konza Prairie Biological Station, Kansas, 1983–2008. Occupancy ( $\psi$ ) was held constant at 1983 levels and detection probability ( $p$ ) was allowed to vary among seasons. Models ranked by the difference ( $\Delta AIC_c$ ) between the model with the lowest Akaike's Information Criterion for small samples ( $AIC_c$ ) and the  $AIC_c$  for the current model ( $K$  = number of model parameters,  $w_i$  = Akaike weight).

Colonization ( $\gamma$ )	Local extinction ( $\epsilon$ )	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$
%Woodland + graze	Graze $\times$ fire freq	33	2,623.2	0.00	0.258
%Woodland + graze	Graze	31	2,624.0	0.81	0.172
%Woodland + graze	Constant	30	2,624.1	1.00	0.158
%Woodland + graze + fire freq	Graze $\times$ fire freq	34	2,625.4	2.26	0.083
%Woodland + graze	Graze + fire freq	32	2,626.2	3.07	0.056
%Woodland + graze	%Woodland + graze	32	2,626.2	3.08	0.055
%Woodland + graze $\times$ fire-return	Graze $\times$ fire-return	34	2,626.7	3.53	0.054
%Woodland + graze	Graze $\times$ fire freq <sup>2</sup>	33	2,628.4	5.22	0.047
%Woodland + fire + graze	%Woodland + fire + graze	34	2,626.5	4.01	0.044
%Woodland <sup>2</sup> + graze	Graze + fire return <sup>2</sup>	34	2,628.5	5.38	0.020
Graze	Graze	30	2,633.1	9.98	0.002
%Woodland <sup>2</sup> + fire-return <sup>2</sup> + graze	%Woodland <sup>2</sup> + fire-return <sup>2</sup> + graze	38	2,637.2	14.00	0.001
%Woodland $\times$ fire-return $\times$ graze	%Woodland $\times$ fire-return $\times$ graze	42	2,636.1	13.54	0.000
Constant	Constant	28	2,645.5	22.80	0.000

coefficients overlapped 0 ( $\beta = 0.87$ , 95% CI =  $-0.63$ ,  $2.38$ ). Local extinction may have been negatively related to average fire frequency at grazed sites ( $\beta = -1.01$ , 95% CI =  $-3.83$ ,  $1.81$ ), whereas ungrazed sites tended to be abandoned if average fire frequency was high ( $\beta = 0.24$ , 95% CI =  $-0.60$ ,  $1.08$ ; Fig. 4B). However, a model where extinction probability was constant over the study period was parsimonious, and model-averaged slope coefficients were not statistically different than 0 (Table 3). We found no evidence that colonization or local extinction were explained by fire-return interval ( $\gamma_{\text{season}}$ ,  $\varepsilon_{\text{season}}$ ) or had a nonlinear relationship with environmental covariates ( $\gamma_{\text{covariate}}$ ,  $\varepsilon_{\text{covariate}}$ ,  $w_i < 0.01$ ; Table 3).

## DISCUSSION

Our study is one of the first analyses of site occupancy dynamics of greater prairie-chickens, and we improve on traditional lek surveys by using occupancy models to correct for imperfect detection rates and to test the effects of environmental factors on the dynamic components of site occupancy. Detection probabilities were imperfect and differed among years, suggesting that analyses of prairie-chicken population dynamics based on lek counts must account for variable rates of detection. Occupancy of prairie-chickens declined by 40% over a 28-year period at Konza Prairie Biological Station, despite protection of the area as a tallgrass prairie preserve managed for ecological research. Declines in site occupancy at  $-3\%$  per year at Konza Prairie were comparable to regional population declines of approximately 2–3% per year based on lek surveys of prairie-chickens in the Flint Hills on private lands managed for cattle production (Applegate and Horak 1999, Rodgers 2010).

### Site Occupancy and Detection

Probability of detection for prairie grouse can be influenced by sex and age of birds, time of day, season, habitat conditions among survey sites, and observer (Walsh et al. 2004, Clifton and Krementz 2006). We used protocols similar to traditional lek surveys and counted prairie-chickens within 3 hr of sunrise on fair-weather days during the spring lekking season when detection should be highest. Nevertheless, our detection probabilities were less than unity ( $p \leq 0.82$ ), variable among years, and not influenced by the number of birds counted at a survey site. Variable detection probabilities unrelated to abundance may be typical for prairie-chickens because birds are conspicuous during breeding displays at leks and in flight, but cryptic while foraging or roosting (Hamerstrom et al. 1957). Naïve estimates of occupancy ( $\psi p$ ), in which detection probabilities were assumed to be fixed, were 30% lower on average than our modeled estimates of site occupancy ( $\psi$ ) but both metrics indicated population declines of similar magnitude. Naïve estimates were more variable (ranging from 0.04 to 0.24) than estimates of site occupancy corrected for imperfect detectability (Fig. 2). Anderson (2001) argued that controlling for probability of detection is necessary if point counts or transect surveys are to be related to population trends.

Our results agree with previous reports of declining numbers of prairie-chickens at Konza Prairie during the 1990s (Zimmerman 1993, Kaufman et al. 1998). Zimmerman (1993) reported more than 200 males attending 13 active leks at Konza Prairie in 1981. Only 12 birds and no leks were observed during surveys in 2008. Unadjusted counts and estimates of site occupancy at Konza Prairie indicated similar rates of decline as annual lek surveys for the entire Flint Hills ecoregion during the same 28-year period (approx. 2–3% per year; Applegate and Horak 1999, Rodgers 2010). Two factors may be contributing to similar rates of decline at Konza Prairie and elsewhere in the Flint Hills. First, prairie-chickens are highly mobile birds with large space requirements (Robel et al. 1970, Schroeder and Robb 1993, Nooker and Sandercock 2008). Despite a relatively large area of 3,487 ha, Konza Prairie may be too small to support a viable population of prairie-chickens if movements between Konza and unproductive populations in adjacent rangelands lead to net emigration (McNew et al. 2011a, b). Second, regional changes that impact grassland birds in the Flint Hills have included increases in woody cover in areas of exurban development with fire suppression, as well as degradation of managed rangelands with frequent fire and more intensive grazing in other areas (Robbins et al. 2002, Briggs et al. 2005, With et al. 2008). Experimental manipulations of fire and grazing at Konza Prairie have provided important insights into the ecosystem function of tallgrass prairie (Knapp et al. 1998), but appear to be negatively impacting habitat suitability for prairie-chickens. Experimental treatments with fire-return intervals  $\geq 10$  years comprise approximately 30% of Konza Prairie and woody cover has increased at a higher rate in these experimental units (approx. 60%) than surrounding rangelands (approx. 40%; T. Prebyl, Kansas State University, unpublished data). Woody encroachment and prairie fragmentation can influence prairie-chickens by affecting settlement decisions or by providing habitat for predators that reduce demographic performance (McKee et al. 1998, Ryan et al. 1998, Kuehl and Clark 2002, Gregory et al. 2011). Overall, our results from a protected prairie preserve indicate that minimizing human disturbance at leks and eliminating harvest are not sufficient to maintain prairie-chicken populations if land cover and land use changes negatively impact habitat quality.

### Colonization and Local Extinction

Occupancy modeling is based on detection-nondetection data but may suggest lines of enquiry into the demographic mechanisms driving changes in population status. Probability of local extinction increased over the 28-year study period and was approximately 6 $\times$  higher than colonization rates at Konza Prairie. Prairie-chickens have high fidelity to lek sites (Nooker and Sandercock 2008), and high rates of site abandonment may indicate that recruitment of prairie-chickens did not offset annual mortality of established birds. Similarly, low rates of colonization may indicate that immigration rates from surrounding rangelands were relatively poor. Results from occupancy modeling were consistent with our demographic data from intensive population

studies of radio-marked prairie-chickens during the past 5 years in eastern Kansas. Population growth rates are currently depressed in the Flint Hills because of low survival among nests, broods, and incubating females, caused primarily by losses to predators (McNew et al. 2011*b*). Taken together, the results of our occupancy and population modeling indicate that prairie-chicken populations are declining at a number of sites within the core of their extant range.

Effective conservation requires an understanding of land cover and land use changes, and we found that different environmental covariates affected the dynamic processes driving site occupancy. Colonization of unoccupied sites was negatively impacted by woodland cover and grazing. Site use by prairie-chickens is likely a tradeoff between the benefits of mating or foraging opportunities versus the costs of predation risk (Gibson et al. 2002, Boyko et al. 2004). Negative impacts of woodland cover are consistent with previous work showing prairie grouse avoid forested landscapes when settling to form new lek sites (Merrill et al. 1999, Niemuth 2003, Gregory et al. 2011). Moreover, survival of prairie-chickens is lower in fragmented grasslands than contiguous grasslands (McNew et al. 2011*b*). Woodland cover negatively affects prairie-chickens because trees provide hunting perches for raptorial birds (Gratson 1988), and edges of woodland habitats are used by foraging mammals (Kuehl and Clark 2002). Colonization was also influenced by grazing management and prairie-chickens were twice as likely to colonize ungrazed than grazed sites. Unburned areas provide taller grasses and more forbs during the late spring and early summer and better cover for birds attending nests, broods, or roost sites (Fuhlendorf and Engle 2001, Robbins et al. 2002). Seasonal productivity of prairie-chickens in eastern Kansas is highest at sites where a mixture of burning and grazing regimes creates heterogeneity in the vertical structure of prairie plants (McNew et al. 2011*b*).

The effects of fire frequency and grazing on site abandonment were less clear. Although there was support for interactive effects of fire and grazing on local extinction, a constant model was parsimonious and model averaged effect sizes were not significantly different than 0. Interactive effects of fire and grazing on local extinction may be explained by the different habitat requirements of males and females, by spatial variation in vegetative cover among experimental sites, or by a combination of these factors (Vinton et al. 1993). For example, tallgrass prairie that is burned rotationally in patches every 3–4 years provides diverse plant communities and greater structural heterogeneity, whereas intervals  $\geq 4$  years lead to woody encroachment (Collins 1987, Briggs et al. 2005, Fuhlendorf et al. 2006). Greater prairie-chickens require a diversity of grassland habitats during their annual life-cycle, and heterogeneity likely benefits persistence of this species (Schroeder and Robb 1993, Patten et al. 2007). Lekking arenas of males are typically in open areas with little residual vegetation, and occur on hilltops in the Flint Hills (Hamerstrom et al. 1957, Patten et al. 2007, Gregory et al. 2011). Females usually nest  $< 3$  km from the lek arenas of males but require sites with adequate cover for reproduction. Production of young is low

in areas where residual vegetation is regularly removed by spring burning or intensive early cattle grazing (McKee et al. 1998, Patten et al. 2007, McNew et al. 2011*a*). Nevertheless, probabilities of local extinction were higher than colonization at all survey sites at Konza Prairie, regardless of management practices; suggesting that prairie-chickens within the preserve were not protected from region-wide population declines. Management actions to conserve prairie-chickens will likely need to occur at larger spatial scales than Konza Prairie.

Fire frequency over the 28-year study period had a greater effect on local extinction than the number of years since a site was last burned. We conclude that long-term fire management has a greater effect on persistence of prairie-chicken populations than short-term changes in treatments. Other species may respond more strongly to short-term changes: Henslow's sparrows (*Ammodramus henslowii*) and grasshopper sparrows (*A. savannarum*) avoid sites treated with spring burning, possibly because nest survival is lower in areas without vegetative cover (Powell 2006, Rahmig et al. 2009). Management for heterogeneity in native prairie may benefit not only prairie-chickens but the entire community of grassland birds.

## MANAGEMENT IMPLICATIONS

Multiseason occupancy models require detection-nondetection data, which are relatively easy to collect and standardize across multiple observers. We suggest that occupancy modeling should be incorporated into monitoring programs for prairie grouse and other sensitive species. Estimation of detection rates would require repeated sampling of a subset of sites but would otherwise require little modification of current survey methods. Land cover and land use change were important correlates of site colonization, and possible correlates of site abandonment, among prairie-chickens at Konza Prairie, and future research should investigate these environmental factors at larger spatial scales within the extant range of the species. At the scale of our survey grids (6.3 ha), the probability of extinction from grazed sites was somewhat reduced with moderate rates of prescribed fire ( $\epsilon < 0.5$  if fire frequency  $> 0.5$ ) and site colonization was poor with even limited numbers of woody plants ( $\gamma < 0.03$  at woodland cover  $> 0.2$ ). Increased application of prescribed burns in areas where forest has exceeded threshold values may do little to improve habitat conditions for prairie-chickens. We recommend tallgrass prairie be managed with combinations of rotational prescribed fire at intervals  $\leq 4$  years and grazing that maintain heterogeneity of native grasslands, prevent establishment of woody plants, and provide diverse habitats for prairie-chickens and other sensitive species of grassland birds.

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